

# NOTES ON THE BEHAVIOUR OF MALES OF PHILANTHUS TRIANGULUM (F.) (HYMENOPTERA, SPHECIDAE)

by

R. T. SIMON THOMAS<sup>1</sup>) & E. P. R. POORTER  
*Pharmacological Laboratory of the University of Amsterdam*

## INTRODUCTION

Fertilized females of *Philanthus triangulum* (F.) (Sphecidae, Hym.) collected in the field can produce normal offspring in the laboratory (Simon Thomas, 1966). However, the females of the first laboratory generation gave rise to a second generation consisting exclusively of males, thus indicating that fertilization had not taken place under the conditions used.

In 1968, 1969, and 1970 the behaviour of females was studied in the field (Simon Thomas and Simon Thomas 1972). Since this investigation provided no information about where and how copulation takes place, the behaviour of the males was also studied. This was done in the summer of 1969 in Les Landes (SW France), in an area where *P. triangulum* occurred in large numbers. In 1970 some additional observations were made by the first author in the same area.

The study area — about one hectare — was situated along a main road (route D 5) near Naboude (see Simon Thomas and Simon Thomas 1972, Fig. 1). A cart track running East-West offered the only bare sand in this area. The vegetation consisted mainly of young pine trees (*Pinus pinaster* Ait.) mingled with various shrubs. Along the main road there were several species of flowers on which the wasps were feeding.

The soil consisted of calciferous fine-grained sand mixed with some humus, and was blackened by resin dust. The nests of the females were only found in the bare sand of the cart rut (Fig. 1). Males were rarely seen in the vicinity; only a few had their sleeping holes in the area. They were seen mainly on flowers along the road and among the bordering vegetation.

To study the males individually, they were marked with a coloured spot of plastic paint on the thorax (Simon Thomas 1970).

Table 1 gives some relevant data on the various observation periods. According to these data, the observations concerned first-generation males only.

Both sexes of *P. triangulum* stay underground at night in burrows dug by themselves or in available holes. The depth of the sleeping holes of the males ranges from 2 to 10 cm, and the entrance is entirely or partly closed from the inside. During the day, the holes of the males are left open.

Most males return day after day to the same sleeping hole and reappear in the morning at varying times. Feeding usually takes place for about an hour in the morning and late in the afternoon and also during additional short periods during the middle of the day (Fig. 2).

<sup>1</sup>) Supported in part by the European Research Office, United States Army, London, United Kingdom of Great Britain.

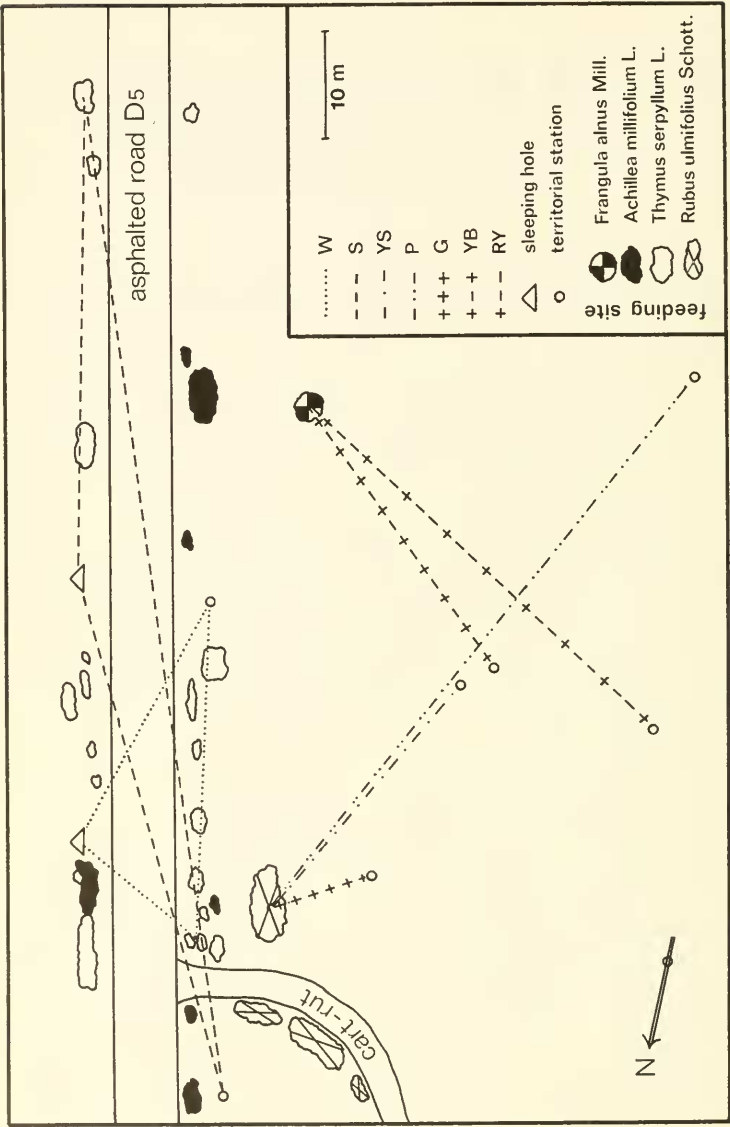


Fig. 1. The study area at Naboude (France); sleeping holes, feeding sites, and territorial stations of seven males of *Philanthus triangulum* (F.) are indicated

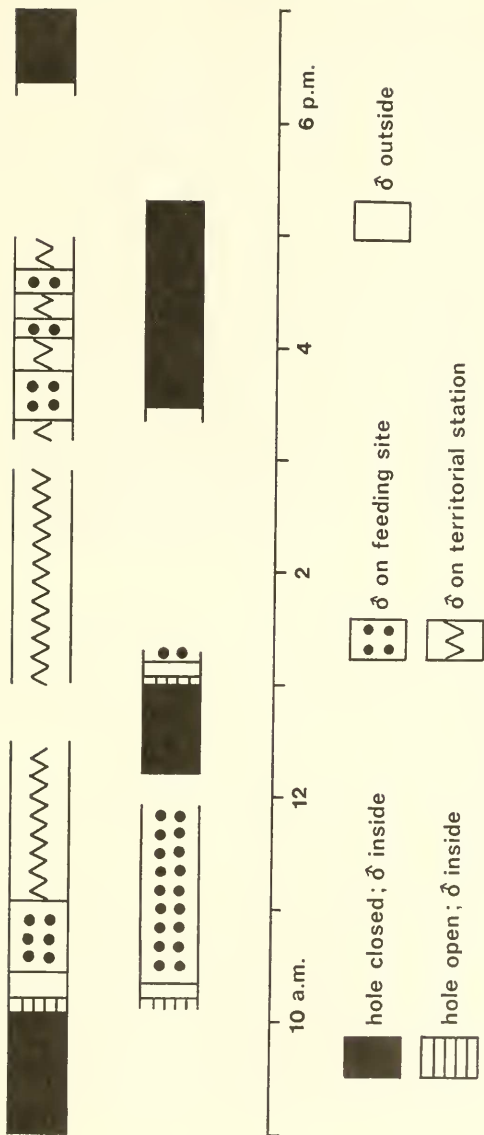


Fig. 2. Activities of a male *Philanthus triangulum* (F.) (W) on June 26th and 30th, 1969

Table 1. Miscellaneous data concerning the three observation periods in Naboude

|                                 | 1968      | 1969      | 1970      |
|---------------------------------|-----------|-----------|-----------|
| Observation periods: males      |           | 25/6—17/7 | 17/6—17/7 |
| Observation periods: females    | 25/6—22/7 | 25/6—5/8  | 17/6—17/7 |
| First male seen in the field    | 12/6      | 22/6      | 19/6      |
| First female seen in the field  | 19/6      | 24/6      | 29/6      |
| First male, second generation   |           | 2/8       |           |
| First female, second generation |           | 4/8       |           |
| Lifespan male (in days)         |           | 33        |           |
| Lifespan female (in days)       |           | 38        |           |

Many males occupy a territorial station and prefer a specific feeding site, which may be located at considerable distance from this station. These observations indicate that individual territorial males are familiar with the location of at least three sites in the field: the territorial station, the feeding site, and the sleeping hole. The locations of the respective sites of seven males are indicated on the map in Fig. 1. The area regularly visited by the animal is a multiple of the size of the territorial area.

Several males return day after day to the same territorial station in the field, usually some small pine tree. They defend these sites against conspecific males and react to other moving insects by flying in their direction. The territorial males confine their attendance and their defensive behaviour to the small tree and its immediate surroundings up to about 50 cm beyond the outer twigs of the three.

## RESULTS

### Position and distribution of territorial stations.

The observation area had a vegetation of grass clumps and shrubs with a scattering of young pine trees. The territorial stations were situated on small pine trees ranging in height from 0.5 to 4 m, except two that were situated in a vegetation of heather and bracken. The territorial stations measured about half a metre. In the choice of a territorial station no preference for a particular type or site of pine tree could be distinguished.

### Behaviour of territorial males in the presence of conspecific males.

The first reaction of the resident male to an intruder is to rush at it. When the intruder turns away and flees, he may be chased by the resident male over a short distance. The latter returns within a few seconds.

When the intruder is unwilling to leave, a complicated conflict may arise in which the males circle around each other in an irregular and jerky manner. The resident male repeatedly takes up a higher position in the air by flying upwards. The upward flight of the resident male is followed by a downward zigzagging swinging flight by which the intruder is re-encountered. The amplitude of this zigzagging decreases gradually. However, the intruder may follow the resident male in the upward flight and in that case the wasps may start circling again. This makes it difficult for the observer to describe the conflict in more detail, because it is impossible to tell the two wasps apart.

When the intruder does not follow the resident male in the upward flight the former either keeps circling or starts hovering below, or it may alight on the substrate of the territorial station. The intruder is usually re-encountered by the resident male when the

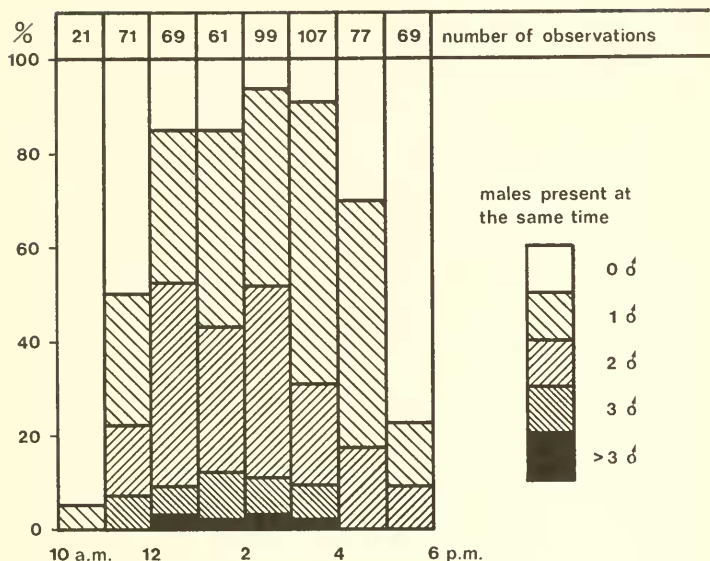


Fig. 3. Relative frequencies of numbers of males at territorial stations in the course of the day

latter comes zigzagging down. When the intruder keeps circling or starts hovering while the resident male flies upward, the former dashes up at the descending resident male. When the intruder has alighted on the substrate of the territorial station it may either be chased away by the descending resident male or dash upward at it. The difference is not always clear to the observer. We observed many zigzagging flights ending in perching of the resident male while the intruder was perched nearby. The repeatedly zigzagging ending in perching was also observed when the intruder had left in the meantime. Physical contact of skirmishing males was never observed.

In a number of cases in which more than two males were present at the same territorial station, small groups of skirmishing males were observed.

#### Attendance at the territorial stations.

Table 2 (data from 1969) shows the highest scores of the total numbers of males recorded simultaneously during the day at the various territorial stations. If one or two of the males were marked, this is also indicated. It is evident that the same territorial stations were often visited by marked males for several days in succession. One male (CW, station 6) attended its territory for a period of at least 14 days. The individually marked males were seldom seen at other territorial stations than their own.



In many cases more than one male was present at the same territorial station. Fig. 3 (data from 1969) shows the relative frequencies of the numbers of males at different hours in the course of the day. For each hour, the data are based on all observations of "no male present", "one male present", etc., at all known territorial stations during the period from June 29th up to and including July 6th, except for June 30th. This was a period without rain and with moderate temperatures (maximum 20°—30° C). Fig. 3 shows that the largest number of simultaneously present males occurred between noon and 4 p.m. In approximately 10 % of the observations during this period, no males were seen.

Table 3 shows the number of times that visiting males were observed at 11 territorial stations between noon and 4 p.m. in the presence or absence of the marked resident males. The numbers in the last column show that in 107 cases the resident male was present without visitors and in 104 cases with one or more visitors. Therefore, visitors were present during 49 % of the observations in which resident males were present.

Table 3. Number of observations at which males were seen in the presence or absence of the marked resident male (M = marked resident male; X = unmarked male) between noon and 4 p.m.

| Territorial station | 2 | 5  | 6  | 7 | 9  | 10 | 12 | 15 | 16 | 17 | 30 |       |
|---------------------|---|----|----|---|----|----|----|----|----|----|----|-------|
| Marked male         | S | YR | CW | G | YS | YB | WG | RY | PG | BR | P  | total |
| M                   | 8 | 26 | 9  | 6 | 3  | 8  | 15 | 9  | 12 | 4  | 7  | 107   |
| MX                  | 4 | 9  | 12 | 3 | 7  | 8  | 6  | 12 | 4  | 12 | 0  | 77    |
| MXX                 | 2 | 3  | 3  | 0 | 6  | 3  | 0  | 2  | 0  | 4  | 1  | 24    |
| MXXX                | 0 | 1  | 0  | 1 | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 3     |
| XX                  | 0 | 0  | 0  | 0 | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 2     |
| X                   | 0 | 0  | 1  | 0 | 2  | 0  | 0  | 1  | 1  | 3  | 0  | 8     |
| no male             | 3 | 5  | 9  | 1 | 3  | 4  | 2  | 3  | 5  | 0  | 6  | 41    |
|                     |   |    |    |   |    |    |    |    |    |    |    | 262   |

When the resident male was absent, there were visiting males in 10 cases and no visitors in 41 cases. Therefore, visitors were present during 20 % of the observations in which the resident males were absent. According to a  $\chi^2$  test, this difference is statistically significant ( $P < 0.0005$ ), and it may therefore be concluded that resident males attract visiting males.

To find out whether residential and visiting males can be distinguished at the stations, 25 unmarked males were caught at 12 territorial stations in the afternoon of July 4th, 1969. The wasps were kept in a cage and supplied with honey and distilled water. The males were marked blue (B\*). One of these received a blue circle on its thorax and was therefore individually recognizable (CB). In the afternoon of July 5th the blue-marked wasps were released. Fourteen of these were seen on July 6th at 13 territorial stations (cf. Table 2). Blue-marked males were seen for a number of consecutive days at 7

Table 2. Attendance of males of *Philanthus triangulum* at territorial stations. The code-letters indicate the presence of individually marked males staying for at least one hour. Code-letters with an asterisk indicate marked males that were not recognizable individually. The figures to the left of the oblique bar indicate the number of observations made between noon and 4 p.m. The figures to the right of the oblique bar indicate the maximum number of males (including marked males) observed at one time. The figures in parentheses (July 4th) are the numbers of unmarked males caught and released as blue males (B and CB) on the afternoon of July 5th.

territorial stations (nos. 9, 10, 17, 26, 27, 28, and 29). It seems likely that the blue-marked males observed at a given territorial station, were always one and the same individual. Since only unmarked males were present at stations 26, 27, 28, and 29 before July 4th, and all unmarked males were captured at these stations, it is likely that the blue males observed afterward were the original territorial males.

At stations 9, 10, and 17, marked territorial males were already present before the blue-marked males were released. These territorial stations were visited during consecutive days by blue-marked males, which eventually replaced the original territorial males.

Station 10, at which no male was caught originally, was occupied by a blue-marked male on consecutive days. Before the afternoon of July 4th it was repeatedly noted that an unmarked male flew to and fro between stations 9 and 10. On July 4th, two unmarked males were caught at station 9. Therefore, one of the males caught at station 9 might have been the future blue-marked male of station 10. At station 17 the original male (BR) was replaced by a blue-marked male on July 6th. On July 8th two blue-marked males were seen here.

These observations indicate that there are two kinds of males, territorial and visiting males. There may be more than one residential male at the same territorial station, but only for a short time.

The fact that only 7 out of the 24 males marked blue were seen again for more than one day, means that most of the blue males were occasional intruders when they were caught. This might also have been the case for several other individually marked males caught in the period from June 27th through July 2nd and which did not return to the station at which they were caught. A few of the latter were later seen occasionally on flowers or near their sleeping holes. Other males appeared to have subsequently established their own territory.

According to the data in Table 2, some territorial stations (11, 14, 24, 30, and 31) were seldom visited by more than one male at the same time, whereas other territorial stations (5, 9, 15, 17, 27, and 34) were visited frequently by several males simultaneously. The preference for certain territorial stations is illustrated by the data obtained at station 27. On July 4th, six unmarked males were caught at this station and since no more males were seen during the rest of the day, these seemed to be all the males present. These six animals belonged to the group of blue-marked males released in the afternoon of July 5th. On July 5th, no males were observed at territorial station 27. On July 6th, two blue males were seen, and on July 7, 8, 9, and 10, one blue male was seen. This latter male may well have been the original resident male. New unmarked males kept being attracted to territorial station 27, and in the period from July 6th through the 10th, this station had the highest score of males simultaneously present of all the territorial stations under study (see Table 2).

The total number of males seen in 1970 in the field was much lower than the figure for the year before. The only territorial station found was closely observed. It was occupied for eleven days (June 24th—July 4th). All visitors were caught and marked individually. During six of these eleven days, one male (OY, marked at this station on June 24th) was seen at this territorial station either alone or with some other males. Six visitors came to this station on July 2nd. Throughout the day, the owner OY was present. On July 3rd another male (caught on blackberry bushes nearby and marked OP) took possession of this territorial station for one day only. On the last day (July 4th), only



two unmarked males were seen at this site. One of the marked visitors (BO) established a new territorial station nearby.

These observations suggest that a male chooses its territorial station more or less at random. Once established, this resident male attracts other males, and these may start new territorial stations nearby.

**Behaviour of territorial males in the absence of conspecific males.**

A territorial station in the pine-clad area usually comprises one or more sites where the animal sits or walks as well as an area around the station used for flying.

When a male is alone at its territorial station it is often perched on a grass blade, pine needle, or some other part of the vegetation but never on the ground. Males may remain perched for periods ranging from a few seconds to several minutes. When a male is perched, his antennae are raised slightly. Perching is regularly alternated with walking and flying. When a male is walking it moves hurriedly up and down grass blades, pine needles, or branches, meanwhile flickering its antennae and tipping the substrate with them. When a male is flying, it moves either in circles around its perch, or from perch to perch, or between different walking sites.

When perching is alternated with flying, the duration of a period of locomotion is relatively short, i.e. 10 seconds or less in 88 % of the observations, 10 to 20 seconds in 8 %, more than 20 seconds in 4 % (50 observations). The maximum duration of one period of locomotion consisting exclusively of flying was 48 seconds.

When locomotion consists of flying as well as walking, the duration of that period is relatively long, less than 10 seconds in 3 % of the observations, 10 to 20 seconds in 9 %, 20 to 50 seconds in 52 %, and more than 50 seconds in 36 % (33 observations). The maximum duration of one period of locomotion was 91 seconds.

We never observed locomotion consisting exclusively of walking. Walking is always interrupted by flying. The duration of periods of walking during this combined type of locomotion was less than 10 seconds in 63 % of the observations, 10 to 20 seconds in 23 %, and more than 20 seconds in 15 % (87 observations), with a maximum of 48 seconds.

**Mating behaviour.**

The first mating was observed on June 29th, 1969 at 4.05 p.m. (31° C). It was carried out by a marked territorial male (YR) at its territorial station (no. 5). During a period of at least 14 minutes before the mating started, no other males were seen at this station. At that time we were recording the activities of the male. Just before the mating occurred, YR had been perched for 56 seconds. It then flew up, and had been circling around the branches of its tree for 9 seconds when a female alighted on a grass blade at a distance of about 75 cm from the flying male. Immediately after the female had landed, YR flew straight at it, made a short turn behind it, and alighted on its back. A few seconds later the male dismounted from the female and turned around. It then became apparent that the male was attached by its genitals to those of the female. The copulating pair faced in opposite directions (almost in a straight line). After 3 minutes and 25 seconds an unidentified fly dashed against the pair, which then flew up in copulating position and was out of sight within a second. Ten minutes later YR was back at its station, but without the female.

The second copulation observed by us occurred on July 2nd at 3.03 p.m. (26° C).

This copulation was also carried out by a marked territorial male (BR) at its territorial station (no. 17). Copulation had already started when we discovered the animals. Disturbed by our arrival, the pair flew off and alighted on a grass blade at the territorial station. After we had taken a photograph, an unmarked conspecific male pounced upon the pair, which caused it to tumble down. The female got grip on a grass blade, but the male hung unsupported from the female with floundering legs. When the female shifted its position, the male obtained support. Shortly afterward, the female wrenched itself free and flew away.

The third copulation was seen outside the main study area on July 11th at 3.30 p.m. (23° C). This pair was disturbed by the observer and alighted on a grass blade still in the copulating position. This copulation too took place at a known territorial station.

In 1970 no mating was observed.

### DISCUSSION

The observations described in the present paper show that males of *Philanthus triangulum* (F.) may possess at least three orientation points at which they are present regularly, viz. a sleeping hole, a feeding site, and a territorial station at which mating was observed. These three sites may be separated by considerable distances.

The behaviour of the males at the territorial stations is of particular interest. In many cases territorial stations were occupied by one and the same male for a considerable period of time, after which another male might become resident at this station.

Besides the resident males, visiting males — often more than one at a time — were present at many territorial stations. This resulted in skirmishes between resident and visiting males, sometimes occurring in small groups.

On three occasions a female was seen to visit a territorial station, and copulation was observed. In two of these cases it could be shown that copulation took place with the resident male.

In analogy with various species of birds, e.g. Black Grouse (*Lyrurus tetrix* L.) and Ruff (*Philomachus pugnax* L.), the males of which display in groups, the territorial stations of *Philanthus triangulum* could be considered "leks", which means display-grounds or arenas. Like those of the above-mentioned birds, the wasps' leks are surrounded by inter-territorial areas.

Our observations of displaying males agree with those of Vergne (1935), who noted groups of male *Philanthus triangulum* on elder bushes in the Botanical Garden of Clermont-Ferrand (France). Beekhuis van Till (1935), on the other hand, saw males dancing in front of the nests of the females in *Het Gooi's Natuurreservaat* in The Netherlands, and also observed copulations near the nests. During extensive observations in Landes (France) from 1968 to 1970 no dancing males, let alone copulations, were ever seen near the nests (Simon Thomas and Simon Thomas 1972).

In the summer of 1970, *Philanthus triangulum* was found again in The Netherlands (Zonderwijk 1971) after an absence of about seven years. This was in Tienraij, in the province of Limburg. On the whole, the behaviour of the males was similar to that observed in France. However, in Tienraij one female nest was found inside a male territorial station. The male frequently tried to copulate when the female passed by in going to or coming from its nest. It is conceivable that Beekhuis van Till saw something similar.

## SUMMARY

To investigate the circumstances under which the copulation of *Philanthus triangulum* (F.) (Sphecidae, Hym.) occurs in the field, the behaviour of the males was studied near Naboude (France).

The males dig individual shallow sleeping holes to which they return every night. They also have special feeding sites. The warmest part of the day is spent at certain other places unrelated to either sleeping or feeding. Observation of marked specimens showed that males occupy these particular spots for a considerable number of days. These site-attached males show territorial behaviour, and they attract other males (visitors), which results in skirmishing between two or more males.

On three occasions females were seen to visit these territorial stations, and copulation followed. In two of these cases it could be shown that copulation took place with the resident male.

## ACKNOWLEDGEMENTS

The authors are greatly indebted to Prof. C. van der Meer, Director of the Pharmacological Laboratory of the University of Amsterdam, for his valuable criticism during the study and for his time-consuming critical reading of the manuscript.

## REFERENCES

- Beekhuis van Till, F. W., 1935, Enige beknopte aantekeningen over het leven van de bijenwolf (*Philanthus triangulum* F.). Maandschrift v. Bijenteelt 38: 258—269.
- Simon Thomas, R. T., 1966, A method of breeding *Philanthus triangulum* F. (Sphecidae, Hymenoptera). Entom. Ber. 26: 114—116.
- , 1970, Het individueel merken van *Philanthus triangulum* (F.). Entom. Ber. 30: 149—152.
- , and A. M. J. Simon Thomas, 1972, Some observations on the behaviour of females of *Philanthus triangulum* (F.). Tijdschr. Ent. 115: 123—139.
- Vergne, M., 1935, Contribution à l'éthologie et au développement post-embryonnaire de quelques Hyménoptères prédateurs (Sphégiens) en particulier de *Philanthus Triangulum* F. Clermont-Ferrand, Imprimerie Moderne, 141 pp.
- Zonderwijk, P., 1971, *Philanthus triangulum* Fabricius (Hym., Sphecidae). Entom. Ber. 31: 79.